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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Southwest)

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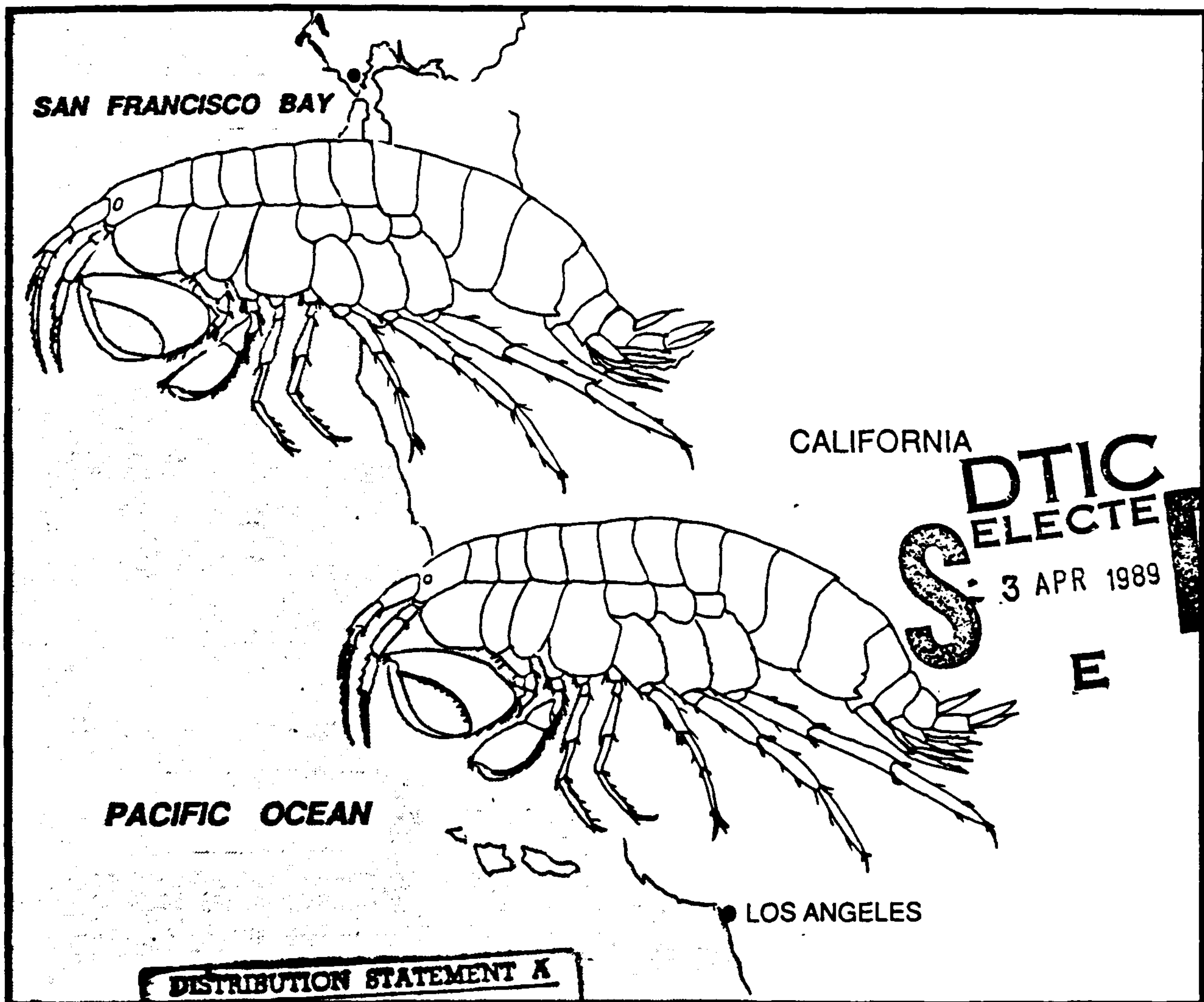

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

Biological Report 82(11.92)
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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Southwest)

AMPHIPODS

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Performed for
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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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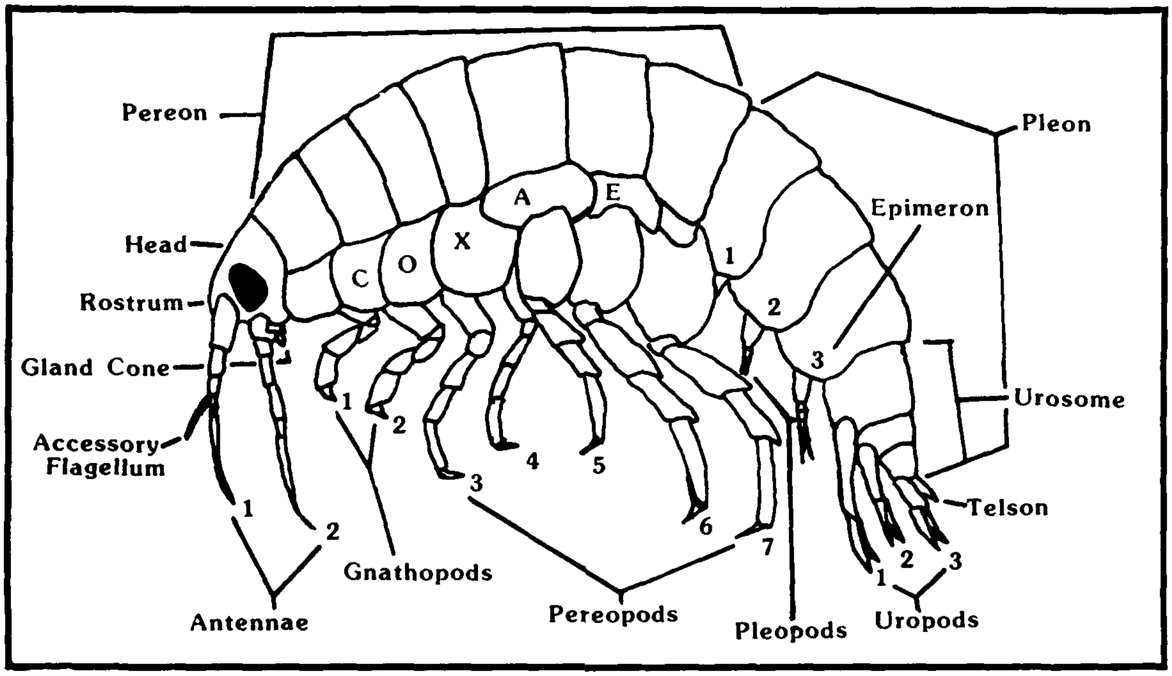

Figure 1. A gammaridean amphipod (from Staude et al. 1977).

AMPHIPODS

NOMENCLATURE/TAXONOMY/RANGE

Scientific name..............Amphipoda
Preferred common name.........Amphipod (Figure 1)
Class........................Crustacea
Subclass..................Malacostraca
Order........................Amphipoda
Suborders......Gammaridea, Hyperiidea, Caprellidea, Ingolfiellidea (Figure 2). Cont'd

Geographic range: This report focuses largely on the suborders Gammaridea and Hyperiidea because of their importance in coastal waters of the Pacific coast region of the Southwestern United States ~~(Figure 3)~~. Many of the California amphipod species are ubiquitous along the Pacific coast and extend northward into Oregon and Washington and southward into Baja California ~~(Barnard 1969a)~~. Gammaridea are the most abundant and diverse group of amphipods. A table of northern and southern amphipods was assembled by Barnard (1969a). More than 25% of the amphipods in California are of unknown geographic affinity. About one-third of southern California species are "cosmopolitan," and one-third of the northern California species inhabit boreal waters of the eastern and western Pacific. The shift from cold-temperate to warm-temperate environments is reflected at Point Conception, which is the northern boundary of many southern species and the southern boundary of many northern species (Barnard 1969a).

-> Keywords: Taxonomy, Crustacea, Reproduction Physiology, Fecundity, Growth Physiology, Fisheries, Dissolved Oxygen, Salinity, Temperature, Water Pollution, Dredging

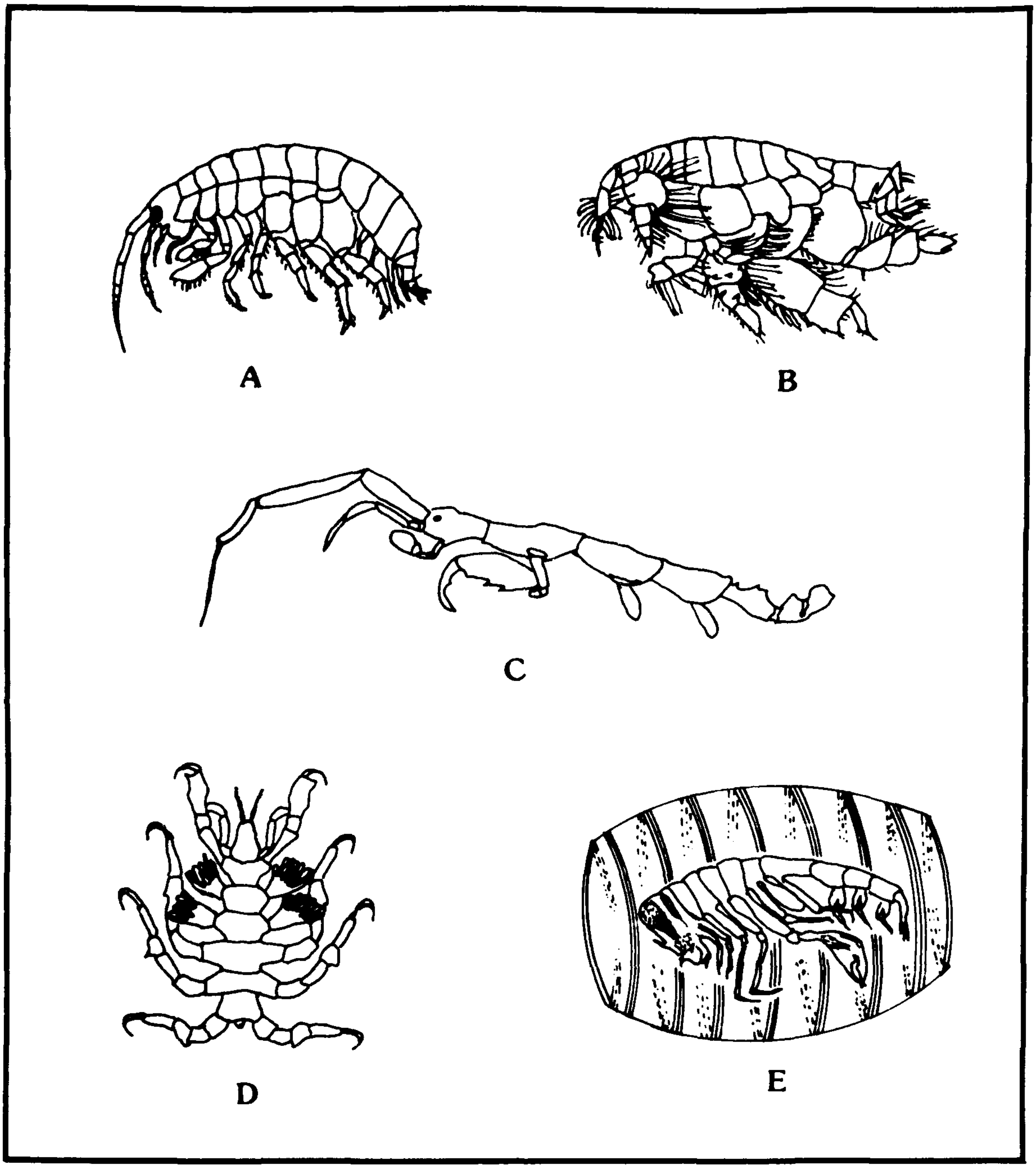

Figure 2. A. Elasmopus sp. and B. Eohaustorius sp., both gammarid amphipods. C. Caprella ferrea, a caprellid amphipod. D. Neocyamus physeteris female, a caprellid amphipod from sperm whale. E. Phronima sedentaria, a hyperiid amphipod that lives inside the tunic of urochordates. (A and B from Barnard 1975; C and D from McCain 1975; E from Barnes 1974. A-D reprinted with permission from the University of California Press; E reprinted with permission from Saunders College Publishing).

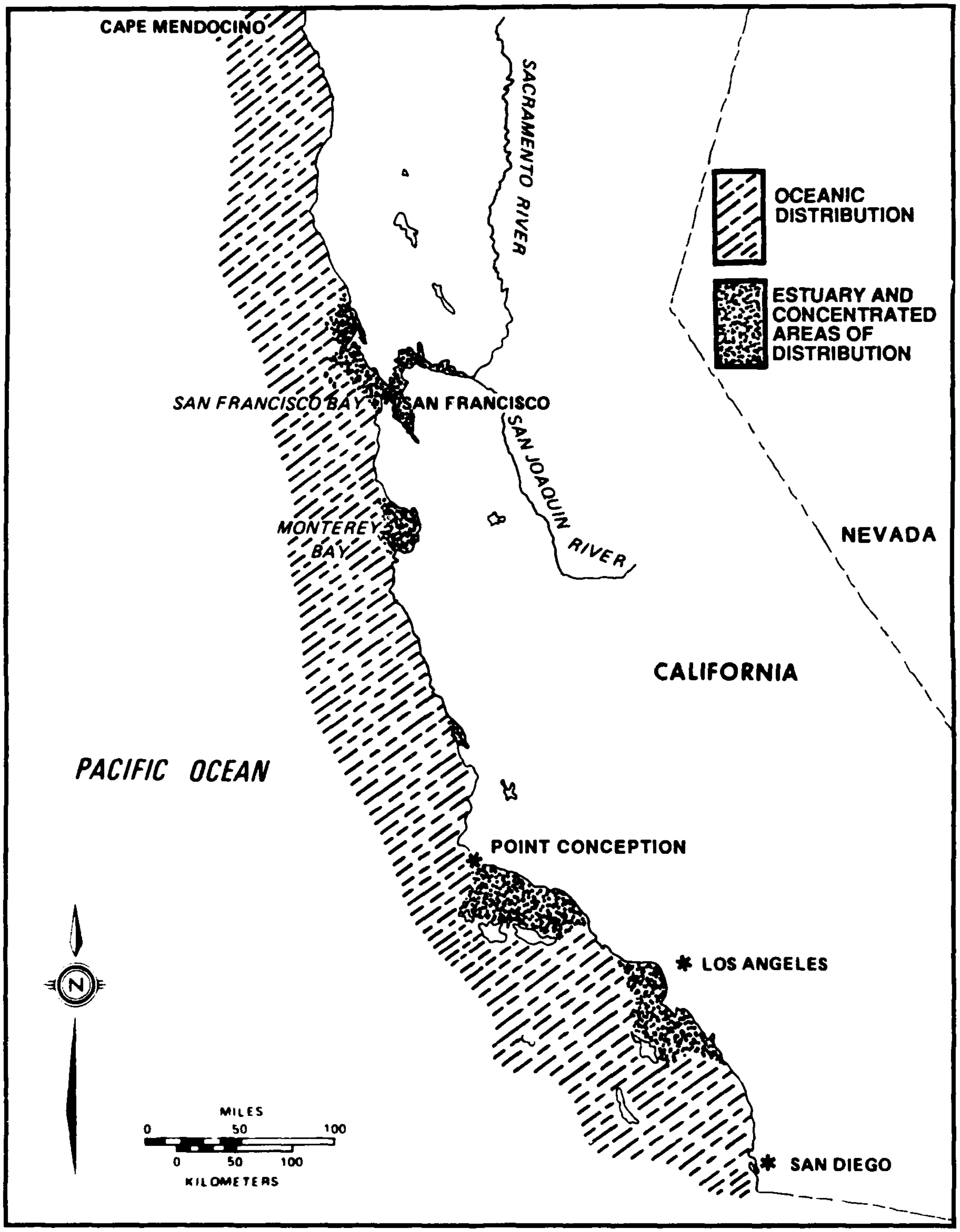

Figure 3. Distribution of the ubiquitous amphipod suborders Gammaridea and Hyperiidea along the coastal areas of the Pacific Ocean off central and southern California.

The generic composition of intertidal amphipods in California overlaps that of similar forms throughout the world (60% with Indo-Pacific tropics, 51% with Japan's Okhotsk Sea, and 46% with the Isle of Man). A total of 174 genera and 1,118 species of rocky intertidal amphipods have been identified north of latitude 45 °S. Sixty-three genera, or about one-third of the world's intertidal genera, are present in California (Barnard 1969b). California's two climates, temperate in the north and subtropical in the south, are one reason for the many known amphipod taxa in that State. Another reason is that amphipods have been studied in far greater detail for many years in California than any other place along the Pacific coast, so there is a more thorough list of taxa. The most abundant species of amphipods in California are frequently in the most diverse genera (primarily marine), although amphipods also inhabit freshwater and some moist terrestrial habitats (Reish and Barnard 1979). The marine forms live at most depths, including deep abyssal waters (Hessler et al. 1978), and in a wide range of habitats. About 40% of the 80 genera of Gammaridea are common worldwide, while the remaining 60% are loosely associated with specific geographical regions or zones (Bousfield 1978).

Gammarid species are found in almost all environments: subtidal, intertidal, freshwater, and terrestrial (Reish and Barnard 1979). The Hyperiidea are entirely marine and pelagic (Bowman and Gruner 1973).

MORPHOLOGY/IDENTIFICATION AIDS

The Amphipoda are distinguished from other crustacea by their unstalked eyes, lack of a carapace, lateral compression of the body, and the structure of the last three appendages (uropods) of the pleon. Amphipods have seven pairs of major thoracic legs (pereopods): the dactyls of the anterior four pair are directed posteriorly, while the dactyls of the posterior legs point anteriorly. Gills are usually present at the base of pereopods 2-6, protected by the ventrally expanded coxal plates. Males and females often can be distinguished morphologically. The head has five fused segments, with two pairs each of antennae and maxillae and a heavily chitinized mandible. There are six or seven freely articulated somites on the thorax (pereon). Plates (coxae) are lateral extensions of the thoracic pereon. Gills (branchiae) are fleshy and plate-like and are attached medial to the second through the sixth coxae on each side. The abdominal region consists of three articulating segments on both the anterior pleon and posterior urosome. The urosome has a terminal telson (Figure 1).

The following key (adapted from Barnes 1974 and Kozloff 1974) is an aid to separate amphipod suborders:

1a. Pereon with seven apparent segments, all having well-developed appendages. Abdomen not vestigial. Body neither slender nor resembling that of a praying mantis ....2.

1b. Pereon with six apparent segments, some of which may have vestigial appendages; abdomen vestigial; head fused with first and second thoracic segment. Body slender and (except for whale lice) resembling that of a praying mantis. Marine. Includes skeleton shrimp .... Suborder Caprellidea.

2a. Eyes generally large, occupying most of head; coxae of pereopods small, often fused with the body; maxillipeds are without palp; last two abdominal segments fused; body more or less transparent. Marine, and usually planktonic or associated with

jellyfish or in tunics of dead salps ...... Suborder Hyperiidea.

2b. Eyes usually present and conspicuous, but not large enough to cover most of the head; coxae of pereopods well developed, usually expanded. Marine, freshwater, and terrestrial ..... Suborder Gammaridea.

2c. Eyes small; body elongate; small coxae; abdominal segments distinct; all but fourth and fifth pairs of abdominal appendages vestigial. Marine, interstitial. Rare ... Suborder Ingolfiellidea.

The most concise identification guides to the marine amphipods of the Pacific Southwest region are those of Barnard (1975) and McCain (1975). Bousfield (1958) may be useful for identifying freshwater gammaridea.

REASON FOR INCLUSION IN SERIES

The benthic amphipods, especially Gammaridea, are an invaluable food source for many economically important fishes (Gerke and Kaczynski 1972; Kaczynski et al. 1973; Mason 1974; Hobson and Chess 1976). Their limited mobility and their sensitivity to environmental changes suggest that their distribution and abundance can be used as an indicator of environmental quality (Albright 1982). Omnivorous and opportunistic feeders such as lysianassids (a gammaridean family) and caprellids recycle detritus and play an important role in the ecosystem by scavenging carcasses of large animals following mass mortalities (Keith 1969; Reish and Barnard 1979). Amphipods, in addition to being scavengers on fish carcasses, are also predatory to some degree on small fishes (Westernhagen and Rosenthal 1976; Hessler et al. 1978; Stepien and Brusca 1985). Hyperiid amphipods are one of the most abundant groups of coastal marine crustaceans (Bowman and Gruner 1973).

LIFE HISTORY

Reproduction and Fecundity

When mating, the male amphipod holds the female in a copulatory embrace (amplexus). Some species have an extended precopulatory ritual (preamplexus), while others do not (Borowsky 1984). In swimming species, the male often carries the female ventrally, or both swim on their sides. Following ecdysis of the female (molting of the exoskeleton), eggs are laid through two ventral pores in the sixth thoracic sternite. Fecundity may exceed 200 eggs per female (Barnard 1969b), but infaunal species tend to have fewer eggs than epifaunal species (Nelson 1980; Van Dolah and Bird 1980). Mature eggs hatch directly into juveniles that resemble adults. These juveniles are usually held in the brood pouch for a few hours to a few days after hatching, then released. They can then feed and return to the pouch for protection (Barnard 1969b; Reish and Barnard 1979).

Information on the reproductive cycles of pelagic species of amphipods is scarce and difficult to obtain in the field. In some hyperiids, the male and female apparently cohabit the same medusa prior to copulation (Sheader 1977). Brusca (1967b) observed several families of pelagic amphipods off the coast of southern California and found that the highest production of ova occurred during the summer and fall months, and that development of the young continued through the following spring and summer.

Growth Characteristics

Amphipod growth rates and lengths vary considerably. Like all crustaceans, amphipod growth takes place at each molt when the old exoskeleton is shed. Amphipods range in length from under 1 cm to about 28 cm, the largest of which is a lysianassid

photographed in the abyssal Pacific Ocean (Hessler et al. 1978). Maximum growth rates of Anisogammarus pugettensis were 4.1% of dry weight per day at 10 °C, increasing more than threefold to 14.3% at 20 °C (Figure 4), with higher growth efficiency at 20 °C (Chang and Parsons 1975). As with most aquatic organisms, temperature has a significant effect on the growth rate. Growth in large (10 mg) individuals of this species was 47% to 72% of food intake when fed Enteromorpha (Chang and Parsons 1975). The growth rate in Gammarus pulex is 63% faster in males than in females, and females achieve a lower final mean weight (52 mg) than males (65 mg), according to Sutcliffe et al. (1981).

Growth is initially rapid in the Gammaridea; molting may begin shortly after hatching and continues through maturity. As amphipods increase in size, molting usually slows to once every 20 to 30 days. The average instar (stage of development between successive molts) lasts 15 days. Gammarids go through at least 12 instars. The maximum life-span estimates are a little more than 6 months in many species, but some polar species are known to live 5 or 6 years. Females commonly lay eggs either during each of the last five or six instars, or at every other instar (Barnard 1969b).

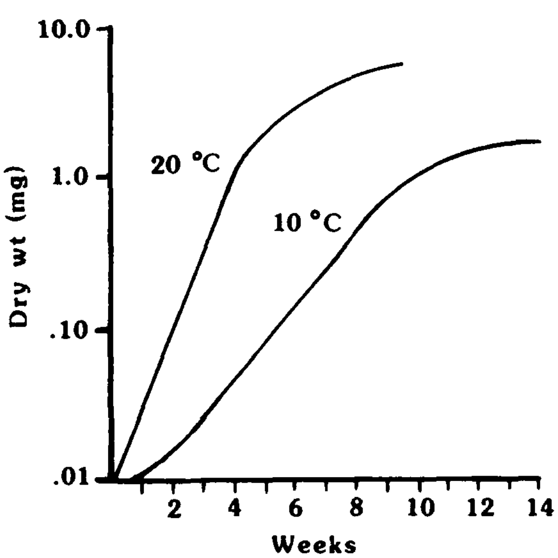

Figure 4. Growth of Anisogammarus pugettensis fed Enteromorpha intestinalis at 10 and 20 °C. (Chang and Parsons 1975; reprinted with permission from the Journal of the Fisheries Research Board of Canada).

Importance to Fisheries

Amphipods are the main food of many species of fish (Kaczynski et al. 1973; Hobson and Chess 1976). Pelagic species sometimes compose the bulk of the diet of herring, mackerel, and Biscayan tunny (Schmitt 1968). Gammarideans, on the basis of an Index of Relative Importance (IRI), were the most important food for nearshore fishes in the Strait of Juan de Fuca. They composed more than half the total food eaten by 38% of the 55 fish species studied (Cross et al. 1978), and they were the most important food of tidepool fishes.

A tube-dwelling gammaridean, Corophium salmonis, is an abundant and preferred prey of chum salmon (Oncorhynchus keta) in the Skagit salt marsh in Washington (Congleton and Smith 1976), as well as in other areas of Puget Sound (Gerke and Kaczynski 1972). Albright (1982) reported that densities of C. salmonis peaked in the tidal flats of Grays Harbor, Washington, in July and August, where they were the dominant organism on mud and muddy-sand bottoms. Densities as high as 57,000/m^2 have been observed (Albright and Rammer 1976). Production from April through September was 3.6-10.7 g dry weight/m^2. According to Albright (1982), C. salmonis is consumed by a large number of fish species (Figure 5), including salmon, sculpins, sticklebacks, gunnels, smelts, cod, sole, flounders, and pricklebacks. Fish that are predators on amphipods and other zooplankton in

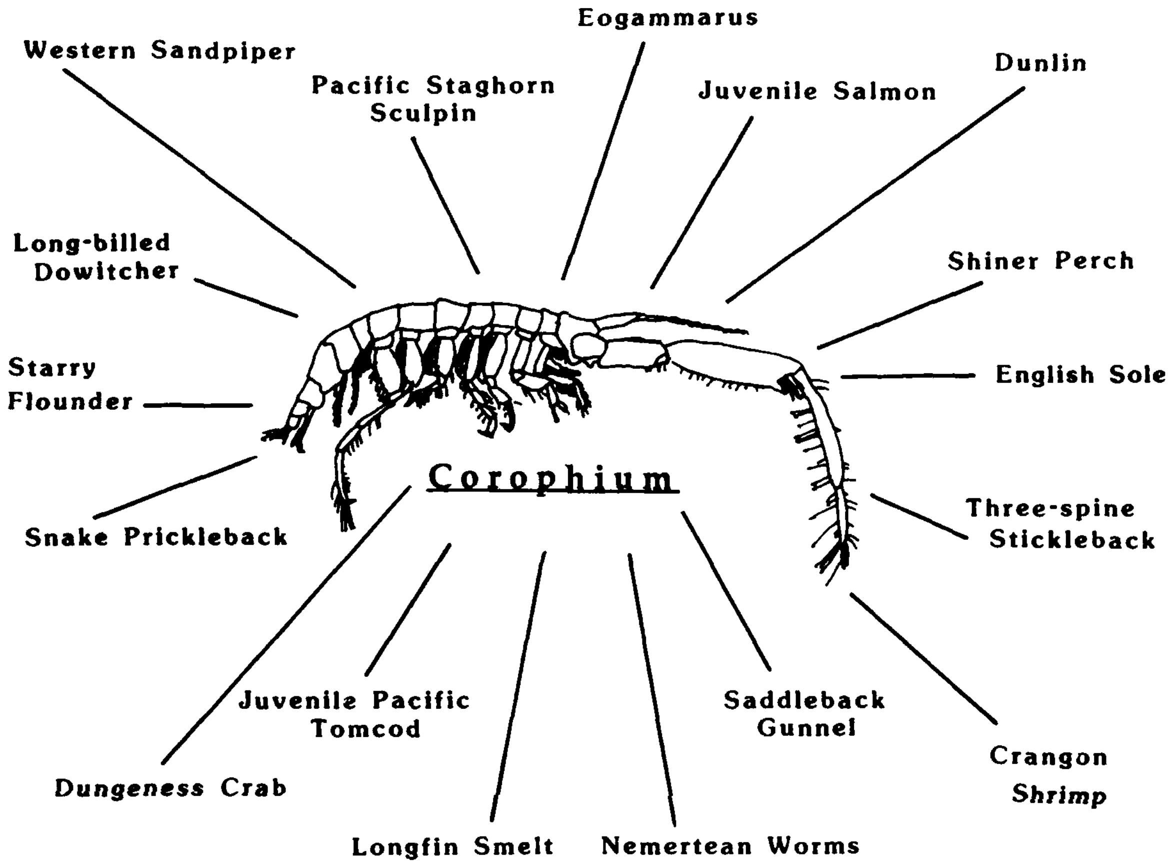

Figure 5. Fish, avian, and invertebrate predators of the amphipod Corophium salmonisi (from Albright 1982).

California have evolved morphologically elaborate feeding mechanisms and body forms; the degree of divergence from the basic body plan depends on how extensively they feed on zooplankton (Hobson and Chess 1976). Crustacean zooplankton, including amphipods, may significantly influence nocturnal versus diurnal distributions and behavior of nearshore fishes of California (Hobson and Chess 1976; Stepien and Brusca 1985).

Two gammarid species have been examined for their potential in fish culture. Mass culture of Anisogammarus pugettensis was proposed by Chang and Parsons (1975) as an alternative to brine shrimp as food for young salmon, but the brine shrimp grew much faster. This gammaridean can tolerate wide ranges of temperatures and salinities and eats a wide variety of plant and animal material, in addition to scavenging dead fish and uneaten fish food in ponds. Gammarus lacustrus, in the shallow prairie lakes of the Hudson Bay drainage, meets dietary requirements for rainbow trout (Salmo gairdneri) that are 5 cm long or longer. These gammarids are easily captured and can be harvested at 1,000 kg wet weight/ha/yr, are equal to or better than available commercial trout feeds, and can improve body coloration and marketability of the fish (Mathias et al. 1982). Gammarus tigrinis, a shoreline

amphipod, has been introduced into brackish streams as food for fishes (Reish and Barnard 1979).

ECOLOGICAL ROLE

Amphipods are considered the most efficient scavengers of sea bottoms and shorelines, where they probably clear up and recycle more organic nearshore debris than any other animal group (Schmitt 1968). Griffiths and Stenton-Dozey (1981) described the importance of the gammarid, *Talorchestia capensis*, in consuming beached kelp in South Africa. This amphipod and dipteran larvae ate 60% to 80% of the beached kelp within 2 weeks, and it is thought that they make a significant contribution (through feces) to organic enrichment in coastal waters.

Numerically, amphipods are the major component of macrofauna on harbor pilings in California. Most are introduced species (carried into ports by foreign vessels) that have had little effect on indigenous amphipods in nearby water (Barnard 1961; Reish 1964). In heavily polluted harbors, amphipods are scarce in both the benthos and on the pilings (Reish 1959).

Beachhoppers of the gammaridean family Talitridae are common on sandy intertidal areas, especially among damp algal debris or wracks (Reish and Barnard 1979). These species are locally transitory because of frequent changes in the tide and wrack accumulations. The maximum density of other amphipods of sandy beaches is related to surf intensity and varies with season (Hughes 1982). The obligate sand-burrowing amphipods belong to two major groups within the family Haustoriidae and are common in southern temperate waters (Bousfield 1970).

Some gammarideans, such as *Ampelisca* sp. and *Photis* sp., construct tubes or cradles on soft or hard substrates (Barnard 1969b). *Corophium* spp., common in estuaries where silting is heavy, form masses of muddy tubes and create currents with abdominal appendages (Albright 1982). The currents are strained by fringes of fine hairs on appendages forward of the abdomen; then the selectively collected material is scraped into the mouth (Kozloff 1973).

Some amphipods inhabit dwellings of other organisms (Kozloff 1973). Many species that are burrowers, such as those of the gammaridean families Haustoriidae, Oedicerotidae, and Phoxocephalidae, have elongated spines or setae on the distal articles of the posterior pereopods that represent an adaptation for burrowing (Reish and Barnard 1979).

Tube-dwelling amphipods almost never dominate a rocky area pounded by waves. Wave action is usually too severe unless protection is given by encrusting organisms. Beds of mussels of the genus *Mytilus* serve as excellent protection for amphipods in rocky intertidal areas (Tsuchiya and Nishihira 1985).

About one-third of all amphipod species in the intertidal areas of California are tube-dwelling forms, compared with only 2% that are sediment burrowers. Phoxocephalids are the major sediment burrowers in the intertidal zone of southern California (Barnard 1969b).

Even among closely related species, amphipods have become highly specialized (Caine 1980). Many intertidal and estuarine amphipods appear to occupy distinct and generally nonoverlapping niches, which may be separated by one or more environmental differences (Bousfield 1970; Caine 1977, 1980; Pinkster and Broodbakker 1980; Gunnill 1984). This separation of niches apparently holds true along the Pacific coast from Washington (Caine 1980) to California (Gunnill 1984).

Examples of amphipods as indicators of environmental conditions are Pontogeneia and Lysianassa, which are typical of sand-encroachment, and Parallorchestes, which is typical of the wave-dash intertidal zone (Barnard 1969b). In areas where these conditions mix, these amphipods, along with Hyale and Aoroides, are all found together. The presence of certain phoxocephalids indicates stratified and relatively undisturbed sediment.

The holdfasts of large kelp (Macrocystis) in the subtidal zone host many species of amphipods, some of which are rare or nonexistent intertidally. An unusually large number of different amphipod species live exclusively or most frequently on kelp holdfasts (Barnard 1969b). Hyale frequens, the most abundant intertidal amphipod in California, lives on or near surf grasses and kelp holdfasts, or in tidepools (Barnard 1969b). Hyale grandicornis lives among algae associated with mussels (Mytilus edulis) and barnacles (Chthamalus challengeri), according to Tsuchiya and Nishihara (1985). It has been observed by Gunnill (1984) that more than one species of amphipod in southern California used the brown alga, Pelvetia fastigiata, but that they occupied different niches--Ampithoe tea, A. lindbergii, and A. pollex lived at the distal ends of the algal fronds, while Photis spp., Corophium spp., and Aorides columbiae lived near the plants' holdfasts.

Coralline stands and sedimentary substrates beneath rocks are poor amphipod habitats. Amphipods that burrow into the substrate have definite preferences for habitats and particle sizes.

Hyperiidea are primarily nektonic, although Hyperia can be taken in benthic samples. They either have well-developed swimming appendages and buoyancy control, or live in association with host medusae or salps (Reish and Barnard 1979). Their feeding habits are poorly understood. Hyperiids may feed on the very organisms that host them, but probably use them more as a base from which to forage; or, they may feed on food captured by the host (Bowman et al. 1963; Patton 1968). In one laboratory study of Lestrigonus sp. and Bougisia sp., food was shared with the host, Leptomedusa sp., when supply was adequate, but when it was not, the amphipods fed on host tissue, starting with the gonads (Bowman and Gruner 1973). Parathemisto sp., a free-living hyperiid, preys on other plankters (Bowman 1960).

A few nektonic gammarideans live in neritic waters. They are either predaceous or are the nektonic mating or dispersal phases of benthic gammarids (Reish and Barnard 1979).

Chelura terebrans, a wood-borer in coastal waters principally south of San Francisco, is the best known amphipod pest. It enlarges holes in wood (e.g., boats and pilings) made by the isopod Limnora sp. (Reish and Barnard 1979).

Swimming among amphipods varies greatly among the various genera. Hyperiidean swimming ranges from the feeble movements of the appendages of Cystisoma sp., to the fast swimming Paraprone spp. which are characterized by a strong pleonal musculature (Bowman and Gruner 1973). Most of the gammarideans--even the burrowing forms--are strong swimmers. The paddling motion of their pleopods is in some cases facilitated by small coupling hooks that join the peduncles of each pair of pleopods. Some gammarids that live on the sea bottom have elongated pereopods that spread out like a spider to prevent them from sinking into the mud. Their bodies hang upside down, giving them a lower center of gravity. This helps avoid displacement by turbulence. Epibenthic gammarids may reduce their susceptibility to predation by swimming. Feller and Kaczynski (1975)

believed that in the spring, juvenile chum salmon in Puget Sound preferred harpactacoid copepods because they were more easily captured than swimming amphipods.

Anisogammarus conferviculus is believed to reduce predation, largely by juvenile chum salmon, through ecological adaptation. Its avoidance behavior includes clumping in refuges with structurally complex habitats, such as bottom vegetation (Levings and Levy 1976). In Grays Harbor, Washington, mature male Corophium salmonis are subject to heavy predation from a variety of sources (Figure 5) beginning in April, when they wander over tidal flats in search of females (Albright 1982). In addition to being prey for many fishes and invertebrates, some pelagic amphipods compose part of the crustacean diet of whales, and the diet of the grey whale along the west coast consists largely of six species of benthic amphipods (Matthews 1978). Amphipods sometimes are eaten by British gulls (Larus sp.) according to Schmitt (1968) and by dunlin (Calidrus alpina) according to Smith and Mudd (1976). Dogielinotus loquax is a prime target for summer shorebird predation (Hughes 1982).

Caprellids, of the suborder which includes skeleton shrimp, are largely intertidal. Their preference of substrate is often specific. They usually cling to living substrate such as kelp, sea grasses, sponges, hydroids, and bryozoans; to a lesser extent, they live on bare sand or mud bottoms (Keith 1971; Caine 1980). They are relatively motionless and feed by grasping food with their free anterior legs and antennae, and holding their position with their posterior legs. Locomotion resembles that of an inchworm with an alternating movement of the front and rear legs (Kozloff 1973). They feed on diatoms, small invertebrates, and detritus, and are in turn the prey of shrimp and many fishes, including cod, blennies, and skates (Keith 1969; McCain 1975; Caine 1977, 1980). Whale parasites (Cyamidae) are also in the caprellid suborder. The genus Cyamus includes about 18 host-specific species. As non-swimmers, they leave the parental brood pouch and dig into the host with hooked dactyls (Schmitt 1968).

It is suggested that the common pelagic amphipod species are more abundant offshore than inshore in oceanic waters and that yearly changes in occurrence and abundance of hyperiid amphipods inshore may be related to coastal upwelling (Lorz and Pearcy 1975). Most hyperiid amphipods live in the upper 100 m of the ocean in the North Pacific central gyre and exhibit diurnal vertical migration (Schulenberger 1978). Off the coast of southern California, both Gammaridea and Hyperiidea have been found at depths greater than 650 m; the depth of their upper limit was defined by the thermocline and the amount of light available (Brusca 1967a). Amphipods from this area exhibit vertical diurnal movements (Brusca 1967a).

ENVIRONMENTAL REQUIREMENTS

Dissolved Oxygen and Temperature

Pelagic gammarid and hyperiid amphipods have been collected in deep, poorly oxygenated scattering layers off southeastern Vancouver Island, British Columbia (Waldichuk and Bousfield 1962). Anisogammarus pugettensis and Allorchestes angustus, both common inshore gammarid amphipods, survive in water with low dissolved oxygen as low as 0.04 ppm at 12 °C near sulfite-rich paper pulp effluent in British Columbia (Waldichuk and Bousfield 1962). The first species is abundant on the bottom at 15 to 22 m; the second species, normally found in shallower waters, was near the surface, perhaps seeking more oxygenated water (Waldichuk and Bousfield 1962). Low oxygen tolerance in either species

remains to be determined, but Chang and Parsons (1975) observed that A. pugettensis survived for several hours at 20% saturation. They also determined a Q_{10} of 1.6, lower than that of other crustaceans, which is generally near 2. (Q_{10} is a measure of the change in physiological processes with temperature. If metabolism (and hence oxygen consumption) doubles when the temperature is increased by 10 °C, an organism has a Q_{10} of 2. If there is no rate change with temperature, the animal has a Q_{10} of 1 and is said to be temperature-independent.) Chang and Parsons (1975) believed this low Q_{10} to be an adaptation of amphipods for coping with rapidly changing intertidal temperatures. Caprellids leave eelgrass beds in Tomales Bay in droves at night when dissolved oxygen concentrations in the beds drop below 2 ppm (Keith 1971).

Tolerances to low oxygen concentrations vary greatly among species. Many are intolerant of low oxygen concentrations, especially species restricted to waters where dissolved oxygen usually is high. Groups such as phoxocephalids (used as indicators of pollution in bioassays) appear much less tolerant to stressful conditions, such as low oxygen concentrations, than many of the species discussed above (R. Albright, University of Washington; pers. comm.).

Caprella laeviuscula and Metacaprella kennerlyi can survive at temperatures as high as 20 °C, while Caprella striata will only survive at temperatures up to 14 °C (Caine 1980).

Salinity

Many species of adult gammarideans withstand high variations in salinity, while some juveniles and embryos are less capable of doing so (although in other species, the juveniles are actually more tolerant than adults). Adults of Corophium volutator, and estuarine species, survived salinities of 2 to 59 ppt (McClusky 1967), but preferred a range of 10 to 30 ppt (McClusky 1970). Adult C. triaenonyx survived in a range of salinities similar to that at which C. volutator survived (Shyamasundari 1973). Although juvenile C. triaenonyx grew at salinities of 7.5 to 37.5 ppt, they survived and grew best at salinities of 20 to 32.5 ppt (Shyamasundari 1973). A. pugettensis, found naturally in salinities of 20 to 28 ppt, cannot survive in freshwater, but can survive at 11 ppt for at least 1 week (Chang and Parsons 1975). Some species of gammaridean genera, such as Gammarus, Hyalella, and Crangonyx, live in freshwater.

In laboratory experiments using estuarine amphipods, Pinkster and Broodbakker (1980) found that (1) survival time of ovigerous females and eggs increased with increasing salinity, (2) males survived better at lower salinities than females, (3) females produced more batches of eggs at higher salinities, (4) time between ovipositions was shorter at higher chlorinities, and (5) females produced more eggs at higher salinities.

Pollution and Dredging

Some amphipod species are more tolerant than others of organic pollution, but the reasons why are not clear (Reish and Barnard 1979). Allorchestes compressa was found to be the species most sensitive to heavy metals among the seven species tested (Reish and Barnard 1979). Capitella, a marine polychaete commonly used as a pollution indicator and generally considered mutually exclusive to amphipods, has been observed in heavily polluted harbors. Capitella also lives in unpolluted deep sea waters near coastal California that are subject to freshwater inflow--habitats where amphipods are notably absent (Reish and Barnard 1979).

The construction of harbors has had little overall effect on amphipod populations native to California

because the animals are so abundant up and down the coast (Reish and Barnard 1979). Nonetheless, amphipods are rare in muddy substrates near docks in Los Angeles, San Francisco, and San Diego (Reish and Barnard 1979). However, delta mudflat areas do contain numerous amphipods; densities of Corophium salmonis become as high as $120{,}000/m^2$ (Smith 1977).

The distribution of Corophium salmonis is influenced by sediment type and depth (it prefers shallow, muddy sand substrates), as well as salinity (Albright 1982). It is thought that dredging likely causes a net short-term reduction in the numbers of Corophium spinicorne, resulting in a substantial impact on its fish and invertebrate predators (Albright and Borithilette 1982). Other species of Corophium are abundant near sewer outfalls, possibly because of organic enrichment (Birklund 1977).

Behavioral changes of amphipods exposed to sublethal quantities of oil have been observed. Populations of intertidal gammaridean beachhoppers are most likely to be affected by oil (Baker 1971), as are populations of subtidal ampeliscids. Dredging is likely to at least temporarily eliminate benthic amphipods that live on or close to the substrate (Albright and Ramer 1976; Reish and Barnard 1979). However, McCaulley et al. (1977) suggest that when dredging occurs, adults of some species are likely to move to nearby unaffected areas and juveniles may rapidly immigrate and repopulate the dredged area.

A recolonization of benthic organisms after attempts at pollution control in the consolidated Slip-East Basin area of Los Angeles Harbor was described by Reish (1959). Although many groups of invertebrates recolonized the area rapidly, amphipods recovered much more slowly. Albright and Borithilette (1982) noted that it may take up to a year to repopulate an area with all the invertebrates that were present prior to dredging, but that opportunistic species such as the amphipods Corophium spinicorne and C. salmonis may repopulate the area much more quickly.

LITERATURE CITED

Albright, R. 1982. Population dynamics and production of the amphipod Corophium salmonis in Grays Harbor, Washington. M.S. Thesis. University of Washington, Seattle. 76 pp.

Albright, R., and P.K. Borithilette. 1982. Benthic invertebrate studies in Grays Harbor, Washington. U.S. Army Corps Eng., Seattle Dist., Contract Rep. DACW67-80-C-0091. 224 pp.

Albright, R., and A.D. Ramer. 1976. Maintenance dredging and the environment of Grays Harbor, Washington. Appendix E: The effect of intertidal dredged material disposal on benthic invertebrates. U.S. Army Corps of Engineers, Seattle District. 244 pp.

Baker, J.M. 1971. Growth simulation following oil pollution. Pages 72-77 in E.B. Coweel, ed. The ecological effects of oil pollution on littoral communities. Institute of Petroleum, London.

Barnard, J.L. 1961. Relationship of California amphipod faunas in Newport Bay and in the open sea. Pac. Nat. 2:166-168.

Barnard, J.L. 1969a. Gammaridean Amphipoda of the rocky intertidal of California: Monterey Bay to LaJolla. U.S. Natl. Mus. Bull. 258. 230 pp.

Barnard, J.L. 1969b. The families and genera of marine gammaridean Amphipoda. U.S. Natl. Mus. Bull. 271. 535 pp.

Barnard, J.L. 1975. Identification of gammaridean amphipods. Pages 313-366 in R.I. Smith and J.T. Carlton, eds. Light's manual: intertidal invertebrates of the central California coast. University of California Press, Berkeley.

Barnes, R.D. 1974. Invertebrate zoology, 3rd ed. W.B. Saunders Co., Philadelphia. 870 pp.

Birklund, J. 1977. Biomass, growth and production of the amphipod Corophium insidiosum (Crawford) and preliminary notes on Corophium volutator (Pallas). Ophelia 16(2): 197-203.

Borowsky, B. 1984. The use of the male's gnathopods during precopulation in some gammaridean amphipods. Crustaceana (LEIDEN) 47(3):245-250.

Bousfield, E.L. 1958. Freshwater amphipod crustaceans of glaciated North America. Can. Field-Nat. 72(2):55-113.

Bousfield, E.L. 1970. Adaptive radiation in sand-burrowing amphipod crustaceans. Chesapeake Sci. 11(3):143-154.

Bousfield, E.L. 1978. A revised classification and phylogeny of amphipod crustaceans. Trans. R. Soc. Can. Ser. 4(16):343-390.

Bousfield, E.L. 1981. Evolution in North Pacific coastal marine amphipod crustaceans in G.G.E.

Scudder and J.L. Reveal, eds. Evolution today. Proc. Second International Congress of Systematics and Evolutionary Biology.

Bowman, T.E. 1960. The pelagic amphipod genus Parathemisto (Hyperiidea:Hyperiidae) in the North Pacific and adjacent Arctic Ocean. Proc. U.S. Natl. Mus. 112(3439):343-392.

Bowman, T.E., and H. Gruner. 1973. The families and genera of Hyperiidea (Crustacea:Amphipoda). Smithsonian Contrib. Zool. No. 146. 64 pp.

Bowman, T.E., C.D. Meyers, and S.D. Hicks. 1963. Notes on the associations between hyperiid amphipods and medusae in Chesapeake and Narragansett Bays and the Niantic River. Chesapeake Sci. 4(3):141-146.

Brusca, G.J. 1967a. The ecology of pelagic amphipods, I. Species accounts, vertical zonation and migration of amphipods from the waters off southern California. Pac. Sci. 21(3):382-393.

Brusca, G.J. 1967b. The ecology of pelagic amphipods, II. Observations on the reproductive cycles of several pelagic amphipods from the waters off southern California. Pac. Sci. 21(4):449-456.

Caine, E.A. 1977. Feeding mechanisms and possible resource partitioning of the Caprellidae (Crustacea: Amphipoda) from Puget Sound, USA. Mar. Biol. (Berl.) 42(3):331-336.

Caine, E.A. 1980. Ecology of two littoral species of caprellid amphipods (Crustacea) from Washington, USA. Mar. Biol. (Berl.) 56(3):327-335.

Chang, B.D., and T.R. Parsons. 1975. Metabolic studies on the amphipod Anisogammarus pugettensis in relation to its trophic position in the food web of young salmonids. J. Fish. Res. Board Can. 32(2):243-247.

Congleton, J.C., and J.E. Smith. 1976. Interactions between juvenile salmon and benthic invertebrates in the Skagit salt marsh. Pages 31-35 in C.A. Simenstad and S.J. Lipovsky, eds. Fish food habits workshop, First Pacific Northwest Technical Workshop, Astoria, Oregon. Oct. 13-15. 193 pp.

Cross, J.N., K.L. Fresh, B.S. Miller, C.A. Simenstad, S.N. Steintort, and J.C. Fegley. 1978. Nearshore fish and macroinvertebrate assemblages along the Strait of Juan de Fuca including food habits of common nearshore fish. NOAA Tech. Memo., ERL MESA-32. 188 pp.

Feller, R.J., and V.W. Kacqunski. 1975. Size selective predation by juvenile chum salmon (Oncorhynchus keta) *on epibenthic prey in Puget* Sound. J. Fish. Res. Board Can. 32(8):1419-1429.

Gerke, R.J., and V.W. Kaczynski. 1972. Food of juvenile pink and chum salmon in Puget Sound, Washington. Wash. Dep. Fish. Tech. Rep. No. 10:1-27.

Griffiths, C.L., and J. Stenton-Dozey. 1981. The fauna and rate of degradation of standard kelp. Estuarine Coastal Shelf Sci. 12:645-653.

Gunnill, F.D. 1984. Differing distributions of potentially competing amphipods, copepods, and gastropods among specimens of the intertidal alga Pelvetia fastigiata. Mar. Biol. (Berl.) 82(3):277-291.

Hessler, R.R., C.L. Ingram, A.A. Yayanos, and B.R. Burnett. 1978. Scavenging amphipods from the floor of the Philippine Trench. Deep-sea Res. 25(11):1029-1047.

Hobson, E.S., and J.R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 74(3):567-594.

Hughes, J.E. 1982. Life history of the sandy-beach amphipod Dogielinotus loquax (Crustacea: Dogielinotidae) from the outer coast of Washington, USA. Mar. Biol. (Berl.) 71(2):167-175.

Kaczynski, V.W., R.J. Feller, J. Clayton, and R.G. Gerke. 1973. Trophic analysis of juvenile pink and chum salmon in Puget Sound. J. Fish. Res. Board Can. 30(7):1003-1008.

Keith, D.E. 1969. Aspects of feeding in Caprella californica Stimpson and Caprella equilibra Say (Amphipoda). Crustaceana 16(2):119-124.

Keith, D.E. 1971. Substrate selection in caprellid amphipods of Southern California, with emphasis on Caprella californica Stimpson and Caprella equilibra Say (Amphipoda). Pac. Sci. 25(3):387-394.

Kozloff, E.N. 1973. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago. University of Washington Press, Seattle. 282 pp.

Kozloff, E.N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle. 226 pp.

Levings, C.D., and D. Levy. 1976. A "bugs-eye" view of fish predation. Pages 147-152 in C.A. Simenstad and S.J. Lipovsky, eds. Fish food habits workshop, First Pacific Northwest Technical Workshop, Astoria, Oregon. Oct. 13-15. 193 pp.

Lorz, H., and W.G. Pearcy. 1975. Distribution of hyperiid amphipods off the Oregon coast. J. Fish. Res. Board Can. 32(8):1442-1447.

Mason, J.C. 1974. Behavioral ecology of chum salmon fry (Oncorhynchus keta) in a small estuary. J. Fish. Res. Board Can. 31(1):83-92.

Mathias, J.A., J. Martin, M. Yorkowski, J.G.I. Lark, M. Papst, and J.L. Tabachek. 1982. Harvest and nutritional quality of Gamarus lacustris for trout culture. Trans. Am. Fish. Soc. 111(1):83-89.

Matthews, L.H. 1978. The natural history of the whale. Weidenfeld and Nicohson, London. 219 pp.

McCain, J.C. 1975. Phylum Arthropoda:Crustacea, Amphipoda: Caprellidea. Pages 367-376 in R.I. Smith and J.T. Carlton, eds., Light's manual: intertidal invertebrates of the central California coast. 3rd ed. University of California Press, Berkeley.

McCaulley, J.E., R.A. Parr, D.R. Hancock. 1977. Benthic infauna and maintenance of dredging. Water Res. 11(1):83-89.

McClusky, D.S. 1967. Some effects of salinity on the survival, moulting and growth of Corophium volutator (Amphipoda). J. Mar. Biol. Assoc. U.K. 48(2):607-617.

McClusky, D.S. 1970. Salinity preference in Corophium volutator. J. Mar. Biol. Assoc. U.K. 50(3):747-752.

Nelson, W.G. 1980. Reproductive patterns of gammaridean amphipods. Sarsia 65:61-71.

Patton, W.K. 1968. Feeding habits, behavior, and host specificity of Caprella grahami on amphipod commensal with the starfish Asterias forbesi. Biol. Bull. (Woods Hole) 134(1):148-153.

Pinkster, S., and N.W. Broodbakker. 1980. The influence of environmental factors on distribution and reproductive success of Eulimno gammarus obstusatus and other estuarine gammarids. Crustaceana Suppl. No. 6:225-241.

Reish, D.J. 1959. An ecological study of pollution in Los Angeles-Long Beach Harbors, California. Occas. Pap. Allan Hancock Found. No. 22:1-119.

Reish, D.J. 1964. Studies on the Mylitus edulis community in Alamitos Bay, California, II. Population variations and discussion of the associated organisms. Veliger 6(3):202-207.

Reish, D.J., and J.L. Barnard. 1979. Amphipods (Arthropoda: Crustacea: Amphipoda). Pages 345-370 in C.W. Hart, ed. Pollution ecology of estuarine invertebrates. Academic Press, New York.

Schmitt, W.L. 1968. Crustaceans. University of Michigan Press, Ann Arbor. 204 pp.

Schulenberger, E. 1978. Vertical distributions, diurnal migrations, and sampling problems of hyperiid amphipods in the North Pacific central gyre. Deep-sea Res. 25(7):605-623.

Sheader, M. 1977. Breeding and marsupial development in laboratory-maintained Parathemisto guadichoude (Amphipoda). J. Mar. Biol. Assn. U.K. 57:943-954.

Shyamasundari, K. 1973. Studies on the tube-building amphipod (Corophium triaenonyx Stebbing) from Visaknapatnam Harbor: effect of salinity and temperature. Biol. Bull. (Woods Hole) 144(3):503-510.

Smith, J.E. 1977. A baseline study of invertebrates and of the environmental impact of intertidal log rafting on the Snohomish River Delta. Wash. Coop. Fish. Res. Unit, Seattle, Final Rep. 77-2. 84 pp.

Smith, J.L., and D.R. Mudd. 1976. Maintenance dredging and the environment of Grays Harbor, Washington. Appendix H: Impact of dredging on the avian fauna in Grays Harbor. U.S. Army Corps of Engineers, Seattle District. 217 pp.

Stanhope, M.J., and C.D. Levings. 1985. Growth and production of Eogammarus confervicolus (Amphipoda: Anisogammaridae) at a log storage site and in areas of undisturbed habitat within the Squamish Estuary, British Columbia. Can. J. Fish. Aquat. Sci. 42(11):1733-1740.

Staude, C.P., J.W. Armstrong, R.M. Thom, and K.K. Chew. 1977. An illustrated key to the intertidal gammaridean amphipods of Central Puget Sound. Coll. Fish. Univ. Wash. Seattle, Contrib. No. 466. 27 pp.

Stepien, C.A., and R.C. Brusca. 1985. Nocturnal attacks on nearshore fishes in southern California by crustacean zooplankton. Mar. Ecol. Prog. Ser. 25(1):91-105.

Sutcliffe, D.W., T.R. Carrick, and L.G. Willoughby. 1981. Effects of diet, body size, age and temperature on growth rates in the amphipod Gammarus pulex. Freshwater Biol. 11(2):183-214.

Tsuchiya, M., and M. Nishihira. 1985. Islands of Mytilus as a habitat for small intertidal animals: effect of island size on community structure. Mar. Ecol. Prog. Ser. 25(1):71-81.

Van Dolah, R.F., and E. Bird. 1980. A comparison of reproductive patterns in infaunal and epifaunal

gammaridean amphipods. Estuarine Coastal Mar. Sci. 11:593-604.

Waldichuk, M., and E.L. Bousfield. 1962. Amphipods in low-oxygen marine waters adjacent to a sulfite pulp mill. J. Fish. Res. Board Can. 19(6):1163-1165.

Westernhagen, H.V., and H. Rosenthal. 1976. Predator-prey relationship between Pacific herring, Clupea harengus pallasi, larvae and a predatory hyperiid amphipod, Hyperoche medusarum. U.S. Natl. Mar. Fish Ser. Fish Bull. 74(3):669-674.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, distribution, life history, and environmental requirements of coastal aquatic species. They are prepared to assist in environmental impact assessment. Amphipods are ubiquitous in distribution, but are most abundant in estuarine areas and other high nutrient areas. Hyperiidea are the third most abundant coastal marine crustacean zooplankton, following copepods and euphausiids. Benthic Gammaridea are an invaluable food source for many economically important fish and invertebrate species. Habitat preference and behavior of the major amphipod groups is highly variable. Intertidal California amphipods overlap the distribution of common genera of other regions around the world. Amphipoda are reported to be indicators of heavily polluted areas. They are considered the most efficient of all scavengers on the sea bottom and in shoreline areas.

17. Document Analysis a. Descriptors

Amphipods
Estuaries
Fish prey
Fisheries
Crustacean zooplankton
Harbor pollution
Feeding habits
Food chains
Sediments
Contaminants

b. Identifiers/Open-Ended Terms

Dissolved oxygen requirements
Salinity requirements
Gammaridea
Temperature
Life history
Hyperiidea
Caprellidea
Growth

c. COSATI Field/Group Ingolfiellidea

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